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Dynamics of estuarine drift macroalgae: growth cycles and contributions to sediments in shallow areas

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ABSTRACT: Blooms of opportunistic macroalgae play a major role in nutrient cycling in shallow coastal areas. However, their short life cycles and rapid biomass remineralization can promote feedbacks on sediment nutrient recycling, leading to self-regenerated blooms and the consequent disruption of local biogeochemical cycles. We investigated the potential for algal biomass–sediment nutrient feedbacks in shallow estuarine areas under natural scenarios of biomass accumulation. To do so, the environmental factors driving the dynamics of drift macroalgal blooms and their biomass contributions to sedimentary organic matter were assessed in a 2 yr field survey in shallow bays of the Patos Lagoon estuary, southern Brazil. Interactive effects of hydrological and water physico-chemical parameters modulated the abundance and persistence of algal biomass. The magnitude of the bloom biomass among bays was positively correlated to wind exposure, reflecting the importance of drifting mat advection by onshore wind-driven waves and currents on biomass accumulation. Large biomass accumulations represented a substantial nutrient stock within the system. However, no significant increases in the sediment total organic carbon or total nitrogen were observed. Isotopic analysis revealed overall low contributions of macroalgal biomass to the sedimentary organic matter during senescence, highlighting possible dual effects of wind exposure on biomass accumulation and deposition. Our findings suggest that, in highly hydrodynamic systems, feedbacks between biomass accumulation and sediment nutrient regeneration are unlikely to occur. Given the unknown fate of algal-bound nutrients, more studies are necessary to determine the effects of drift macroalgae-dominated phases on the long-term balance of nutrients within the estuarine system.

KEY WORDS: Macroalgal blooms • Hydrology • Wind exposure • Sedimentary organic matter • Fate of nutrients • Patos Lagoon

INTRODUCTION

In shallow coastal areas worldwide, an increasing trend in the frequency of blooms of fast-growing ephemeral macroalgae, also known as green tides, has been observed. Blooms of opportunistic macroalgae, such as some species of *Ulva* and *Cladophora*, can outcompete other autotrophs such as seagrasses and microphytobenthos for nutrients and light, causing shifts towards the dominance of ephemeral primary producers (Lyons et al. 2014). While nutrient enrichment is recognized as a primary cause of the excessive growth of ephemeral macroalgal species, the onset and magnitude of the bloom may be triggered by the interactive effects of water physico-chemical and hydrodynamic conditions (Martins et al. 1999, 2007). In shallow estuarine waters, the growth of macroalgae is controlled by the availability of light at the bottom, water temperature and salinity, but the conditions for bloom formation depend on the water residence time, which can enable or prevent the retention and accumulation of the biomass produced (McGlathery et al. 2007).

Most green tides are composed of macroalgal mats that are detached from the substrata due to waves and current action (hereafter termed ‘drift macroalgae’). Due to their low erosion thresholds, drift macroalgae can be easily transported as bedloads (i.e. mats drifting over the sediment surface) or as floating mats in the water column (Flindt et al. 2004) by tidal and wind-driven currents and waves (Biber 2007, Keesing et al. 2011). Consequently, local tidal cycles and wind regimes can determine the occurrence and magnitude of the accumulations of the macroalgal biomass produced in shallow bays and estuarine shoals (Kennison & Fong 2013).

Once established, macroalgal blooms play a major role in nutrient cycling, acting initially as a nutrient sink. Opportunistic macroalgae such as *Ulva* exhibit high uptake efficiency of dissolved organic and inorganic nutrients from the water column and sediments (Tyler et al. 2003, Fong et al. 2004). However, due to their ‘boom and bust’ life cycles and high biomass

turnover rates ranging from days to a few weeks, drift macroalgal blooms do not represent a long-term nutrient reservoir (McGlathery et al. 2007). During biomass active growth, senescence and collapse, the assimilated nutrients can be rapidly recycled in the water column as dissolved organic nitrogen and particulate organic nitrogen, where they are partly processed by the microbial loop, mineralized or transferred to higher trophic levels through grazing (Tyler et al. 2001, Fong et al. 2004).

While a large bulk of the algal tissue is recycled in the water column, part of the material contributes to temporary increases in the sediment organic matter content during bloom collapses (Pihl et al. 1999, Corzo et al. 2009, Hardison et al. 2010, Gao et al. 2013). The highly labile dead biomass is rapidly decomposed (Banta et al. 2004), increasing pore water nutrients through bacterial activity and promoting subsequent effluxes of nutrients across the sediment–water interface (García-Robledo et al. 2008, 2013, Hardison et al. 2010, Gao et al. 2013). Therefore, the rapid regeneration of nutrients may help initiate the further growth of macroalgae that, along with the mats continually drifting in from surrounding areas, help sustain the large accumulations of ephemeral macroalgae. This self-regeneration mechanism may cause the reoccurrence of macroalgal blooms and lead to the disruption of local biogeochemical cycles in shallow estuarine areas (Sundbäck et al. 2003).

To investigate the potential of self-regeneration by drift macroalgal blooms, most studies have focussed on macroalgal nutrient removal and regeneration in the water column (e.g. Tyler et al. 2001, Fong et al. 2004). More recently, attention has turned to the sedimentary processes that link nutrient uptake in the water column to remineralization and release in the sediment during biomass deposition and senescence (e.g. Corzo et al. 2009, Hardison et al. 2010, García-Robledo et al. 2013). However, most of these studies have been conducted in micro- and mesocosm experiments, over short spatial and temporal scales. Consequently, factors that affect both the spatio-temporal patterns of drift macroalgal blooms and their subsequent contributions to sedimentary organic matter have not been considered at a field scale. This knowledge gap, concerning the potential feedbacks of green tides on estuarine biogeochemical cycles, limits our current understanding of the processes contributing to the occurrence and fate of drift macroalgae.

In the last decade, the Patos Lagoon estuary (PLE) in southern Brazil has undergone ecological changes, including reductions in the distribution and abundance of submerged aquatic vegetation (i.e. *Ruppia maritima* meadows) and increases in the abundance of drift macroalgae (Odebrecht et al. 2010). Shifts towards the macroalgae-dominated state have mainly been related to changes in the hydrological conditions (Lanari & Copertino in press), but may also be associated with the increasing trend in the inorganic nitrogen concentrations in the water column and in the sediment pore water (e.g. Baumgarten & Niencheski 2010). Local biogeochemical studies have shown that the estuarine sediments recycle a significant portion of the primary production, subsequently providing inorganic nutrients to the water column (Niencheski & Jahnke 2002). However, the role of drift macroalgae in estuarine nutrient cycling is still poorly understood.

To assess the role of drift macroalgal blooms on estuarine nutrient cycling, we investigated the drivers of temporal and spatial variability in the occurrence and magnitude of drift macroalgal blooms in shallow estuarine areas based on 2 main hypotheses. First, we hypothesized that while drift macroalgal blooms result from the coupling of factors affecting both drifting biomass production and retention in the system, the spatial variability in the timing and magnitude of biomass accumulations relies on wind exposure. Second, using the natural patterns of drift macroalgal bloom occurrence and persistence in the study area, we tested the hypothesis that drift macroalgae are an important source of sedimentary organic matter. We suggest that the contribution of macroalgae to the sediments may be proportional

to the magnitude of the biomass accumulations, possibly creating conditions for feedbacks on sedimentary nutrient regeneration that trigger self-regenerated blooms.

MATERIALS AND METHODS

Study site

The warm temperate Patos Lagoon is one of the largest choked coastal lagoons in the world (10360 km²; 30° 12' to 32° 12' S, 50° 40' to 52° 15' W; Fig. 1a). The estuarine area (PLE; ~1000 km²) is influenced by a microtidal regime (~0.47 cm), further attenuated by a single and narrow entrance channel (0.5 to 3 km wide); therefore, the hydrology of the PLE is primarily controlled by fluvial discharge and wind patterns (Möller et al. 2001). The prevailing northeast (NE) winds in spring and summer and southwest (SW) winds in autumn and winter force the outflow and inflow, respectively, of water between the estuary and the coastal region. During flood periods (mainly in winter/spring), the PLE becomes a river-dominated system, remaining fresh for several months (Möller et al. 2001). Conversely, during low freshwater discharges (summer/autumn), southerly winds promote saltwater intrusions, blocking freshwater outflow and increasing water retention within the estuary (Odebrecht et al. 2015). Therefore, marine and euhaline conditions usually occur in summer/autumn, while oligohaline conditions prevail in winter/spring. Overall, high levels of nutrients in the water column (up to 40 µM NO₂⁻+NO₃⁻, 40 µM NH₄⁺ and 8.7 µM PO₄³⁻) and sediment (up to 710.7 µM NH₄⁺ and 14.6 µM PO₄³⁻) are maintained through inputs from the watershed, macrophytes and anthropogenic sources (Baumgarten & Niencheski 2010, Odebrecht et al. 2010).

From August 2012 to August 2014, macroalgal blooms and their contributions to sedimentary organic matter were investigated in shallow shoals with different levels of exposure to the prevailing SW and NE winds. Within each wind direction, 2 sites were selected according to an *a priori* contrast between low (hereafter shelter-NE and shelter-SW) and moderate to high exposure (exp-NE and exp-SW; Fig. 1b). The wind exposure of sites was determined according to their average wave fetch values and their wave exposure (Burrows et al. 2008; Fig. 1b). Wave exposure was determined based on a 200 m grid-based map of the PLE obtained from the high-resolution shoreline (GSHHS) digital coastline dataset (www.ngdc.noaa.gov/mgg/shorelines/gshhs.html). For all coastal cells in the grid, the number of 200 m grid cells representing water surface (i.e. sea cells) was calculated in 16 angular sectors (22.5° each) and summed up. Therefore, for each coastal cell, wave exposure gradient is given as the number of surrounding cells that do not represent land masses (i.e. land cells), thus being available for wind drag on the water surface.

Hydrological and meteorological factors

Information regarding local freshwater discharge was provided by the Brazilian National Water Agency (www.hidroweb.ana.gov.br). The sum of the flow of the 3 main rivers was assumed to be a proxy for the total Patos Lagoon freshwater discharge (Möller et al. 2001). Data on hourly wind speed and direction, obtained at the mouth of the PLE, were provided by the Rio Grande Maritime Pilotage (www.rgpilots.com.br/).

Water physico-chemical parameters

The estuarine water level (fixed ruler) in relation to the mean water level of the lagoon (40 cm) was obtained daily in an area approximately 3 km from the studied sites within the Brazilian Long-Term Ecological Research Program (www.peld.furg.br/index.php/metadados). Water salinity, temperature, turbidity (Multiparameter HI9829, Hanna Instruments) and

Secchi depth were monitored weekly at each site from August 2012 to August 2014. Water samples (N = 3) were collected monthly from each site for the analysis of dissolved inorganic nutrients (NH₄⁺, NO₂⁻, NO₃⁻ and PO₄³⁻). Underwater photosynthetically active radiation (PAR) at the bottom (I_z) was estimated according to the Lambert-Beer equation:

$$I_z = I_0 \times e^{-kz} \quad (1)$$

where I_0 is the PAR at the surface, k is the light extinction coefficient ($k = 1.7 \times \text{Secchi}^{-0.85}$; Costa & Seeliger 1989), and z is depth. We assumed that PAR is 50% of the overall available energy for photosynthesis and a 5% decrease in the incident light at the water surface (da Silva & Asmus 2001). Data on the hourly surface radiation in the study area were provided by the Brazilian National Institute of Meteorology (www.inmet.gov.br/portal).

Macroalgal and sediment sampling

To assess the occurrence and magnitude of drift macroalgal blooms at each sampling site, macroalgal cover was measured monthly along 3 transects (200 m each) laid out perpendicular to the coast, 100 m apart from one another. Drift macroalgae coverage was estimated by visual census within 4 quadrats (0.25 m²) at 50 m intervals (N = 20 per transect). Each 50 × 50 cm quadrat was divided into 4 smaller ones (i.e. 12.5 × 12.5 cm, representing 25% coverage each) using lateral marks. Smaller quadrats were further mentally subdivided into 4 subquadrats. The total of subquadrats covered by drift mats was summed up, and coverage was thus determined at 6.25% increments. When biomass coverage was far below 6.25%, it was assigned as 1%; otherwise, it was considered 6.25%. We used a PVC cylinder (176.62 cm²) to sample macroalgal biomass at 10 points where the coverage was 100%. To evaluate the role of algal biomass as a source of sedimentary organic matter through elemental and isotopic analysis, samples of the surface sediment (N = 3) were collected with a cylinder core (8 cm diameter, 3 cm depth) from below macroalgal mats within the transect area and placed in amber glass vials. The macroalgal and sediment samples were transported on ice to the laboratory and prepared within the next 1 to 2 d.

In the laboratory, the macroalgae were cleaned by removing associated fauna and detritus and rinsed with tap and distilled water; the dry weight (48 h at 60°C) was then determined. Subsamples (N = 3) of ~100 g fresh biomass were separated for elemental and isotopic analysis (see below for further details) and for taxonomic identification. For the latter, subsamples were fixed in a 4% formalin solution, and identification was based on morphological features. The average biomass (g dry weight [DW] m⁻²) for each site was estimated by multiplying the biomass values by the mean percentage cover of the survey area estimated by visual census (N = 60 quadrats).

Elemental and isotopic analysis

The sediment and macroalgal biomass subsamples were dried to a constant weight (48 h at 60°C) and ground to a fine powder using a mortar and pestle. Subsamples were weighed (25–30 mg for sediments and 2.5–3.0 mg for macroalgae) and pressed into tin capsules for the analysis of total organic carbon (TOC), total nitrogen (TN) and their isotopic composition (δ¹³C and δ¹⁵N). The sediment samples were analysed for TOC, TN, δ¹³C and δ¹⁵N for the sheltered sites (shelter-NE and shelter-SW) from August 2012 to August 2013 and up to August 2014 for the exposed sites (exp-NE and exp-SW). The δ¹³C and δ¹⁵N of the macroalgal biomass were analysed only for 2014. The elemental and isotopic analyses were performed using an automatic elemental analyser (2400 Series II CHNS/O System, Perkin-Elmer) and a mass spectrometer (Stable Isotope Laboratory, University of Georgia, USA), respectively. Previous studies in the PLE have shown that sediments contain insignificant

amounts of sedimentary calcium carbonate. Claudino et al. (2013) tested the need for a decarbonation treatment of PLE sediments and found no difference in the $\delta^{13}\text{C}$ value between acidified and non-acidified samples. Therefore, our sediment samples were not acidified prior to the analysis. Quality control for the elemental analysis of the macroalgal tissue was conducted using the certificate reference material acetanilide and the sediment MESS-3 (National Research Council Canada). The percent TOC and TN content in the macroalgal tissue and sediment were converted to molar TOC:TN ratios, and the isotope ratios were expressed as parts per thousand (‰). Pee Dee Belemnite was used as the standard for carbon, and atmospheric nitrogen was used for nitrogen. Based on the standard deviation of the internal standard replicates, the analytical precision for the carbon and nitrogen content and their isotopes was ± 0.16 , ± 0.05 , ± 0.08 and ± 0.12 , respectively.

Data analysis

Variation in water salinity has been used as a proxy for the water retention time in the study area (e.g. Odebrecht et al. 2015). Similarly, we used the average salinity and its variability (i.e. coefficient of variation, CV) across season as a proxy for water retention within the estuary. In general, periods of higher water retention were identified by increases in salinity associated with a low CV, which reflected transitions from periods of outflow to inflow and the persistence of meso/euhaline waters in the estuary (Odebrecht et al. 2015).

Intercorrelations among freshwater discharge, level, salinity (mean and CV), turbidity, irradiance, temperature, NH_4^+ , NO_2^- and NO_3^- (expressed as dissolved inorganic nitrogen, DIN) and PO_4^{3-} were analysed through principal component analysis (PCA). Since no significant spatial differences were found in the water physico-chemical parameters (level, salinity, turbidity, temperature and nutrients; see Fig. S1 in the Supplement at www.XXXXXXX), the abiotic data were averaged across all sites. All variables except irradiance were log-transformed to achieve a normal distribution. The abiotic parameters were grouped along the PCA axis according to their eigenvector coefficients. This procedure provided ecological meaning for the PCA components and allowed data reduction. The relationships between the averaged macroalgal biomass across sites and the hydrological and water physico-chemical parameters were thus investigated through multiple regression analysis using the eigenvalues of PC1, PC2 and PC3 as independent variables which explained, respectively, 47.10, 17.40 and 15.21% of the data variability. The residuals were checked for data homoscedasticity and normality. Spatial patterns of the distribution and abundance of drift macroalgal biomass among sites were analysed in relation to the local wind direction, frequency and speed.

The contributions of drift macroalgal biomass to the organic matter in the sediments were estimated using the Bayesian mixing model MixSIAR (Stock & Semmens 2013). The MixSIAR model provides estimates of the relative contributions of distinct sources to a mixture even in undetermined systems, taking into account the uncertainty associated with both sample variability and unknown sources of error (Parnell et al. 2013). The mixing model was run for each season using the sampling sites as fixed factors. The sedimentary organic matter sources were suspended particulate organic matter (SPOM), drift macroalgae, the seagrass *Ruppia maritima* and the saltmarsh plants *Spartina densiflora*, *Scirpus maritimus* and *S. olney* (Table 1). Seasonal elemental and isotopic values for *R. maritima*, *S. densiflora*, *S. maritimus*, *S. olney* and SPOM in the study area were obtained from Claudino et al. (2013). *R. maritima* and *S. densiflora* presented similar isotopic signatures and were pooled as a single source. Due to their similar photosynthetic pathways, *S. maritimus* and *S. olney* were also pooled together and denoted as C3 plants. TOC and TN were informed for each source. Discrimination effects were not included due to the lack of significant changes in the

elemental and isotopic values of the sources during diagenesis in the study area (data not shown). The posterior distributions of organic matter sources were calculated using long Markov chain Monte Carlo chains (chain length = 1000000, burn-in = 700000, thin = 300), and convergence was checked through diagnostic tests (see Stock & Semmens 2013 for more details).

RESULTS

Temporal variation in hydrological and water physico-chemical parameters

Water discharge, retention, level, salinity, turbidity and irradiance showed a strong seasonal trend throughout the studied period (Fig. 2a,b, Table 2) and were highly correlated along the first principal component (PC1; Table 3). PC1 reflected the associated changes in water physico-chemical parameters related to water retention, therefore representing the balance between outflow (i.e. freshwater discharge) and inflow (i.e. saltwater intrusion) in the PLE. Periods of high freshwater discharge, predominantly in winter and spring, were followed by increases in water level and turbidity and decreases in salinity, underwater irradiance and water retention (i.e. indicated by high salinity CV values). Water temperature varied seasonally, with the lowest values recorded during winter, and was positively correlated with PC2 (Fig. 2c, Table 3).

Nutrient concentrations in the water column showed no consistent seasonal trend (Fig. 3 and Fig. S1). Peaks of NH_4^+ were found mainly during October and November 2012 (spring; Fig. 3a). Higher concentrations of $\text{NO}_2^- + \text{NO}_3^-$ were observed during October and November 2012 (austral spring), from April to July 2013 (autumn to winter) and in July 2014 (mid-winter; Fig. 3a). The variability in the PO_4^{3-} concentrations was less pronounced, although an increasing trend towards autumn and winter of 2014 was observed (Fig. 3c). All nutrient concentrations increased along PC3 (Table 3).

Temporal and spatial dynamics of drift macroalgal blooms

Annual and interannual variability in the abundance and composition of drift macroalgae were found. Mixed mats of tubular *Ulva* species (formerly *Enteromorpha*) occurred during summer/autumn 2013 and autumn/winter 2014, while mats dominated by *Rhizoclonium* sp. occurred only in autumn/winter 2014. *Polysiphonia* sp. occurred at negligible abundances in summer 2013 and was not considered in the total algal weight. Peaks of biomass occurred during early summer and autumn 2013 and in autumn and early winter 2014 (Fig. 4a). The average biomass values across all sites ranged from 0.38 g DW m⁻² (winter, August 2012) to 566 g DW m⁻² (winter, June 2014) and, overall, higher mean biomass values were found during 2014 (223 g DW m⁻²) compared to 2012–2013 (43 g DW m⁻²). The results of the regression analysis showed that PC1, representing freshwater discharges and associated changes in water retention and physico-chemical parameters, was the best predictor of the average values of drift macroalgal biomass ($R^2 = 0.67$, $F_{7,12} = 3.55$, $p = 0.02$). On the other hand, no significant effects of water temperature (here represented by PC2) or nutrient concentrations (PC3) on drift macroalgal abundance were detected. Macroalgal tissue TOC and TN presented slight spatial differences (see Fig. S2 in the Supplement) and were averaged across all sites for analysis. The mean values for C content varied from 31.5% (March 2014) to 39% (July 2014), and N content ranged from 1.5% (December 2013) to 3.6% (November 2013; Fig. 5a). Temporal changes in the algal tissue C:N ratios reflected variation in the drift macroalgal abundance, with peaks during bloom periods (Fig. 5b).

We found marked spatial variability in the timing and magnitude of drift macroalgal blooms. The exposed sites showed the highest values of biomass throughout the studied period, with

algal accumulations forming persistent, extensive patches covering up to 90% of the surveyed area (Fig. 4a,b). Conversely, sheltered sites showed lower values of accumulated biomass deposited onto the substrata as scattered thin patches. Temporal shifts in biomass accumulation between the exposed sites were in accordance with the local wind patterns (data presented in Fig. S3 in the Supplement). The largest algal blooms at the exp-SW site occurred during autumn (March to May) 2013 and 2014 under an increasing frequency and intensity (from 2.1 up to $>11 \text{ m s}^{-1}$) of winds from the SW quadrant. Conversely, the exp-NE site showed large algal blooms, mainly in summer 2013 (December to February) and early winter 2014 (June), under the predominance of moderate (5.7 to 8.8 m s^{-1}) to strong (8.9 to 11.1 m s^{-1}) N to E winds.

Contribution of drift macroalgal biomass to sediment organic matter

Sediment elemental and isotopic values showed no clear seasonal or spatial trends (Fig. 6a–d), indicating that algal biomass did not promote significant increases in sedimentary organic matter. Accordingly, the mixing model results showed that drift macroalgae, with isotopic signatures varying from -13.5 to -17.5‰ for $\delta^{13}\text{C}$ and 7.4 to 8.2‰ for $\delta^{15}\text{N}$ (Table 1), had a much lower contribution ($3.56 \pm 2.96\%$; mean \pm SD across all sites and seasons) to the sedimentary organic matter compared to other sources such as SPOM ($54.14 \pm 29.40\%$), *S. densiflora* and *R. maritima* ($30.24 \pm 19.34\%$) and C3 plants ($11.68 \pm 11.10\%$; Fig. 7).

In spite of the large credible intervals, the highest average values of contributions of macroalgae to the sedimentary organic matter across all sites occurred during summer ($4.5 \pm 0.36\%$) and winter ($8 \pm 2\%$) 2013 and autumn ($6.4 \pm 2.4\%$) and winter ($4 \pm 2.26\%$) 2014, periods of the highest macroalgal biomass accumulation (Figs. 4a,b & 7). The only exception to this pattern was winter 2013, a post-bloom period. However, there was a spatio-temporal decoupling between algal contributions to the sediments and the observed patterns of drift macroalgal abundance. Algal contributions were not proportional to the annual and interannual variations in algal bloom magnitude and persistence. Furthermore, the largest biomass blooms at exposed sites were not translated into the higher values of organic matter incorporated into the sediments. Indeed, the values of algal contribution to the sedimentary organic matter were not significantly different among the exposed and sheltered sites.

DISCUSSION

Our results showed that interactive effects of hydrological and meteorological factors create favourable conditions for the onset of large drift macroalgal accumulations in shallow areas. Nonetheless, regardless of their magnitude and persistence, macroalgal blooms made a minor contribution to the sediment organic matter pool compared to other primary producers, such as seagrasses and salt marsh plants. These findings contrast with those from previous experimental studies showing that drift algae may make significant, although transitory, contributions to the sedimentary organic matter (e.g. Corzo et al. 2009). Most of these previous studies, however, did not take into account the natural patterns in their abundance and their driving factors (but see Pihl et al. 1999). Therefore, our study highlights the importance of considering the environmental context in the assessment of macroalgal bloom feedbacks on benthic nutrient regeneration.

Temporal and spatial patterns of drift macroalgal blooms

Drift macroalgal blooms have been a common feature in the PLE in the last decade, suggesting a shift towards a macroalgal-dominated state (Lanari & Copertino 2017). Although opportunistic macroalgal blooms are often regarded as a symptom of eutrophication (Teichberg et al. 2010), we did not observe significant effects of water column nutrients on

the development of macroalgal biomass on a monthly basis (i.e. PC2; Figs. 3 & 4a). However, the tissue TN values found here were close to or above the critical values required for maximum growth (i.e. 2.2%; Pedersen & Borum 1996) and those found under nutrient-enriched conditions (i.e. 3.5%; Martinetto et al. 2011), highlighting that nitrogen availability was sufficient to trigger drift macroalgal blooms. The largest blooms in 2014 coincided with a period of increased PO_4^{3-} concentrations in the water column (Figs. 3c & 4a,b), indicating that in nitrogen-enriched systems such as the PLE, phosphorus supply may limit the growth of bloom-forming macroalgae (Teichberg et al. 2010).

The effects of nutrient availability on bloom onset are also mediated by local hydrology, which in turn controls the variability in water physico-chemical parameters in the PLE. During very high freshwater discharge (spring 2012 and late winter/spring 2013; Figs. 2a & 3), water level and turbidity increase, which reduces the light levels in the water column and limit the growth of algae (Lanari & Copertino 2017). Conversely, low/moderate freshwater discharges and increased saltwater intrusions and water retention (i.e. summer/autumn 2013 and autumn/early winter 2014; Fig. 2) improve underwater light conditions through decreased water turbidity and levels. Together with the reduced currents, the latter conditions enable biomass growth and accumulation in shallow areas. Blooms of *Ulva* species benefit from increased salinity and temperature in summer/early autumn (Coutinho & Seeliger 1986, Martins et al. 1999), whereas *Rhizoclonium* sp. thrives at lower salinities, temperatures and irradiances in mid-autumn to winter (Hall & Walmsley 1991, Matsuyama-Serisawa et al. 2004). Thus, seasonal differences in the timing, persistence and composition of blooms reflect the annual and interannual variability in the local hydrology and covarying water physico-chemical parameters.

Bloom-forming species may be an important food resource for some consumers in the mudflats of the PLE during warmer seasons (Claudino et al. 2013). Juvenile and adult crabs, such as *Neohelice granulata* and *Callinectes sapidus*, are found grazing on drifting mats in shallow areas (M. Copertino pers. obs.). Nonetheless, bloom-forming macroalgae do not contribute significantly to the diets of herbivorous fish in the PLE (Mont'Alverne et al. 2016, Garcia et al. 2017). As in many temperate estuaries, the PLE harbours few species of herbivorous fish and crustaceans (Mont'Alverne et al. 2016), and herbivory therefore cannot control macroalgal blooms. Furthermore, top-down controls on algal blooms can be limited under nutrient-enriched conditions, such as in the PLE (e.g. Martinetto et al. 2011).

Exposure had a positive effect on the magnitude of algal blooms, with the site of the largest biomass accumulations varying seasonally according to the prevailing NE and SW winds. Large drift mat accumulations occur at exposed shallow bays due to their import from nearby areas in addition to the retention of *in situ* growth (Berglund et al. 2003). Accordingly, the average wind speeds observed here (6 m s^{-1}) were within or above values reported to trigger onshore algal transport/accumulation in coastal areas worldwide through wind-induced waves and superficial currents (i.e. 5 to 10 m s^{-1} in China, Keesing et al. 2011; 3–5 m s^{-1} in Denmark, Rasmussen et al. 2013). Thus, our findings indicate that interactive effects of exposure and local wind patterns can cause predictable patterns of biomass accumulation in shallow estuarine areas.

However, the low spatial replication here limited our conclusions. Drift mat advection and accumulation may also co-vary with other factors such as substratum complexity (e.g. presence of seagrass meadows; Biber 2007) and bottom topography (Kotta et al. 2008). Consequently, contrasting effects of exposure on drift macroalgae accumulations have been reported (e.g. Pihl et al. 1999, Berglund et al. 2003, Rasmussen et al. 2015), and studies conducted over large spatial scales are needed to test the generality of our results.

Contribution of drift macroalgae to sediment C and N

Ephemeral macroalgal blooms are short-lived (McGlathery et al. 2007). Accordingly, senescent understory biomass was observed within bloom periods, corroborating the short life cycles (~12 d for *U. clathrata*; Copertino et al. 2009) and high decomposition rates (~4 wk in litter bags; data not shown) of the opportunistic species observed in the PLE and reported elsewhere (e.g. Castaldelli et al. 2003, Conover et al. 2016). Although increases in sediment C and N content can result from macroalgal biomass depositions and senescence (Pihl et al. 1999, Corzo et al. 2009, Hardison et al. 2010), our results did not support these findings. No significant increases in sediment TOC and TN were observed, regardless of the temporal and spatial differences in the magnitude of biomass accumulations.

Many factors may have resulted in transitory increases in sedimentary organic matter of a few days or weeks that could not be detected at the monthly time scale adopted in our study (Rossi 2007, García-Robledo et al. 2008). Due to the fast turnover of opportunistic macroalgal detritus, biomass deposited on the sediment is quickly recycled through bacterial assimilation, resulting in effluxes of ammonium (NH_4^+), nitrite (NO_2^-) and nitrate (NO_3^-) across the sediment–water interface (García-Robledo et al. 2008, 2013). In shallow estuarine areas similar to the PLE, wind action maintains high oxic conditions at the water–sediment interface, thus enhancing the microbial mineralization of organic matter and its transfer to the water column (Rigaud et al. 2013). Nutrients released from sediment can be assimilated by microphytobenthos (Hardison et al. 2010), which is subsequently consumed by surface deposit feeders, transferring nutrients from the sediment to secondary consumers (Rossi et al. 2007). Indeed, transitory increases (i.e. 2 wk) in sedimentary TOC (1.7 to 14%) and TN (13.5 to 16%) have been observed during experimental additions of low algal biomass (e.g. ~ 40 g DW m^{-2} , Rossi et al. 2007; 220 g DW m^{-2} , García-Robledo et al. 2008). Nonetheless, at higher levels of biomass accumulation such as those found here, up to 1900 g DW m^{-2} , biomass inputs would override sediment mineralization rates, thereby causing C and N accumulations and increasing the potential for algal biomass feedbacks on nutrient cycling (Rossi 2007).

No evidence of macroalgal C and N accumulation was observed. The stable isotope analysis showed that, overall, the low sedimentary TOC and TN contents were explained by a low incorporation of algal biomass, regardless of the magnitude and persistence of the accumulations. The incorporation of algal biomass within sediments relies on the existence of hydrodynamic conditions promoting the deposition and burial of macroalgal tissue (Hardison et al. 2010). We suggest that, although advective transport may promote large accumulations of drift biomass in shallow shoals, the driving force behind its accumulation, i.e. wind action, also hampers its deposition and burial within sediments during senescence. The low erosion thresholds of drift mats cause their frequent translocation by waves and currents (Flindt et al. 2004), leading to unstable deposition on the sediment surface at small spatial (i.e. 1 m^2) and temporal scales (i.e. a few hours to a few days; Biber 2007, Rasmussen et al. 2013).

Accordingly, wind-driven weekly variation in the spatial distribution of drift macroalgae has been reported in shallow shoals of the PLE (Lanari & Copertino 2017), indicating transitory mat depositions on the sediment surface. In addition, although decaying biomass was detected during the sampling periods, the relocation of drift mats may have alleviated extensive biomass die-offs through shelf-shading, diminishing mass transfers to superficial sediments (García-Robledo & Corzo 2011). Therefore, our study indicates that in high hydrodynamic systems where unstable depositions of algal mats occur, feedback mechanisms between algal blooms and nutrient regeneration within sediments are unlikely to occur.

As algal blooms had a minor contribution to the sediment organic matter pool, the fate of nutrients bound to algal biomass in the PLE is still unclear. Dense biomass accumulations

comprise a substantial stock of labile organic matter with high nutritional value (Banta et al. 2004, Britton-Simmons et al. 2012). For instance, biomass peaks of up to 982 g DW m⁻² with a nitrogen content of 2.1% (i.e. exp-SW in autumn 2014) can store up to 0.18 t N ha⁻¹. Simultaneously, biomass accumulated through mat advection may promote influxes of macroinvertebrates from adjacent areas and enhance the biotic structural complexity in shallow areas, increasing macrofaunal diversity and abundance (Salovius et al. 2005). Under the maintenance of oxic conditions, herbivory and detritivory may partly account for the recycling of organic matter, thus creating hotspots of secondary productivity in areas of algal accumulations (Cebrian et al. 2014). Released organic and inorganic nutrients in the water column during biomass senescence and decomposition can also be taken up by other primary producers, such as salt marsh plants (Newton & Thornber 2013) and phytoplankton (Wang et al. 2012), or may sustain further macroalgal growth (Hanisak 1993).

Macroalgal-bound nutrients were ultimately flushed out from shallow areas by increased freshwater discharges (i.e. winter 2013 and 2014). In the absence or loss of perennial primary producers that promote long-term nutrient retention, such as seagrasses, the mass export of plant-bound nutrients may be enhanced (Flindt et al. 2004, McGlathery et al. 2007). The advection of drift biomass from shallow areas may fuel deep secondary production through substantial fluxes of energy and nutrients to recipient communities, creating spatially subsidized food webs (Britton-Simmons et al. 2012, Hyndes et al. 2014). However, low contributions of drift macroalgae to herbivores and detritivores occurring in deeper areas have been reported in the PLE (Mont'Alverne et al. 2016). Thus, according to the hydrological (Britton-Simmons et al. 2009) and basin-shape conditions (Britton-Simmons et al. 2012, Filbee-Dexter & Scheibling 2016), much of the biomass advected to deep channels can be exported to adjacent coastal areas, hence representing nutrient loss from the system (Martins et al. 2007). If so, eutrophication in shallow areas may ultimately cause a long-term oligotrophication of the system (McGlathery et al. 2007, García-Robledo & Corzo 2011).

In conclusion, our study highlights the role of drift macroalgal blooms as either a sink or source of nutrients within a subtropical, highly dynamic estuarine system. The combined effects of local hydrology, water physico-chemical parameters and wind action promote large algal biomass accumulations representing short-lived nutrient stocks in shallow areas. Although nutrient regeneration within sediments can sustain the onset of macroalgal blooms (Sundbäck et al. 2003), our findings indicate that feedbacks of biomass accumulations on sedimentary organic matter are unlikely to occur due to the dual effects of wind action on mat accumulations. Therefore, meteorological and hydrodynamic conditions must be considered when assessing the fate of algal-bound nutrients in shallow coastal areas. To evaluate the generality of our results, more studies assessing the incorporation of algal biomass within sediments under distinct spatio-temporal scales of mat deposition are needed, preferably using additional tracers. Moreover, as the fate of macroalgal-bound nutrients is still unclear, investigations on the effects of algal-dominated phases on nutrient cycling and transfers across different biotic compartments and at distinct spatial scales (i.e. shallow and deep areas) may provide insights on nutrient balance within the ecosystem.

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Fig. 1. (a) Patos Lagoon estuary along the southern Brazilian coastline and (b) the mesomixohaline area of the estuary, with coastal wave exposure highlighted by colours; wave fetch values of each sampling site are indicated. Sampling sites are indicated by squares (circles) for sites with preferential exposure to SW (NE) winds. Filled and empty symbols represent exposed and sheltered sites, respectively. Wave exposure gradients for each coastal cell are given in grid cell units which represent the number of 200 m grid cells covered by sea and available for calculating wind drag on the water surface in 16 angular sectors of 22.5°

Fig. 2. Variation of the hydrological and physico-chemical parameters. (a) Freshwater discharge, water level and salinity, (b) water column turbidity (FNU: formazin nephelometric units) and irradiance, and (c) temperature from August 2012 to August 2014. Values are means (\pm SE) among all sites. W: winter, Sp: spring, Su: summer and Au: autumn

Fig. 3. Monthly variation in (a) NH_4^+ , (b) $\text{NO}_2^- + \text{NO}_3^-$ and (c) PO_4^{3-} concentrations in the water column between August 2012 and August 2014. Values are means (\pm SE, N = 12) among all sites. W: winter, Sp: spring, Su: summer and Au: autumn

Fig. 4. Temporal variation in drift macroalgal (a) biomass and (b) coverage among sites from August 2012 to August 2014. Values are means \pm SE (N = 10 and 60 per station for biomass and coverage, respectively). Note the broken y-axis in panel a. DW: dry weight, W: winter, Sp: spring, Su: summer and Au: autumn. Sites were labelled according to low ('shelter') and moderate to high exposure ('exp') and wind direction (northeast: NE, or southwest: SW)

Fig. 5. Monthly variation in (a) total organic carbon (TOC) and total nitrogen (TN) and (b) C:N molar ratios in algal tissue between August 2012 and August 2014. Values are means (\pm SE, N = 12) among all sites. W: winter, Sp: spring, Su: summer and Au: autumn. Note the broken x-axis depicting only drift macroalgal blooming periods

Fig. 6. Monthly variation in (a) % total nitrogen (TN), (b) % total organic carbon (TOC), (c) $\delta^{15}\text{N}$ and (d) $\delta^{13}\text{C}$ in sediment sampling sites from September 2012 to August 2014 (at sites exp-SW and exp-NE; site abbreviations as in Fig. 4) and from September 2012 to August 2013 (shelter-SW and shelter-NE). Values are means \pm SE

Fig. 7. Estimated contributions of (a) drift macroalgae, (b) *Ruppia maritima* and *Spartina densiflora*, (c) C3 plants and (d) suspended particulate organic matter (SPOM) to sedimentary organic matter among sites from spring 2012 to winter 2014. Bars represent the posterior probability means \pm 95% credible intervals. Site abbreviations as in Fig. 4. W: winter, Sp: spring, Su: summer and Au: autumn. Note the different y-axis scales

Table 1. Mean values (± 1 SD) of $\delta^{13}\text{C}$, $\delta^{15}\text{N}$, %C and %N for the sources *Ulva* sp. and *Rhizoclonium* sp. (drift macroalgae), *Ruppia maritima*, *Spartina densiflora*, *Scirpus maritimus* and *Scirpus olney* and suspended particulate organic matter (SPOM) collected in mudflats of the Patos Lagoon estuary, Brazil, across seasons (spring, summer, autumn and winter). Lowercase letters indicate sources grouped for mixing models analysis. ND:

	Summer				Autumn				Winter				Source
	$\delta^{13}\text{C}$	$\delta^{15}\text{N}$	%C	%N	$\delta^{13}\text{C}$	$\delta^{15}\text{N}$	%C	%N	$\delta^{13}\text{C}$	$\delta^{15}\text{N}$	%C	%N	
Drift macroalgae	-15.7 ± 1.5	8.2 ± 1.4	33 ± 0	1.9 ± 0	-17.5 ± 1.6	7.5 ± 0.9	34.1 ± 3	3.4 ± 1.4	-13.5 ± 3.3	7.4 ± 1.3	36.5 ± 2	3 ± 1	Claudino et al. (2013), this study
<i>Spartina densiflora</i> ^a	-12.1 ± 0.2	6.2 ± 0.5	41 ± 1.4	0.7 ± 0.2	-12.3 ± 0.3	6.2 ± 0.7	40.7 ± 0.7	0.8 ± 0.2	-12.2 ± 0.6	4.5 ± 0.6	40.6 ± 1.2	0.9 ± 0.1	Claudino et al. (2013)
<i>Ruppia maritima</i> ^a	-10.5 ± 1.4	7.3 ± 0.4	40.3 ± 1.6	3.2 ± 0.4	-13.9 ± 0.9	7.2 ± 0.8	28.6 ± 4	2 ± 0.1	-10.7 ± 1.2	6 ± 0.8	41 ± 2.1	3.8 ± 0.7	Claudino et al. (2013), this study
<i>Scirpus maritimus</i> ^b	-25.2 ± 0.9	7 ± 0.5	41.7 ± 1	1.3 ± 0.2	-28.1 ± 0.6	5.7 ± 0.8	39.9 ± 1.9	2.2 ± 0.1	-27 ± 1.1	4 ± 2.1	41.3 ± 1	1.6 ± 0.3	Claudino et al. (2013)
<i>Scirpus olney</i> ^b	-26.7 ± 1	6 ± 0.5	39.8 ± 1.5	1.5 ± 1.1	ND	ND	ND	ND	-28 ± 1.1	6 ± 1.2	40.3 ± 0.2	1.5 ± 0.2	Claudino et al. (2013)
SPOM	-18.4 ± 0.4	6.6 ± 0.3	1.8 ± 0.1	0.2 ± 0	-19.5 ± 1.3	1.8 ± 1.6	0.9 ± 0.5	0.2 ± 0.1	$-18.5^c \pm 0.8$	$4.2^c \pm 0.9$	$1.4^c \pm 0.3$	$0.2^* \pm 0$	Claudino et al. (2013)

^aDenoted as a single source due to the similarities in their isotopic signature

^bDenoted as a single source (C3 plants) due to their same photosynthetic pathway

^cValues are averages between summer and autumn

Table 2. Mean, standard deviation (SD) and coefficient of variation (CV) of water salinity from Spring 2012 to Winter 2014

Year	Spring			Summer			Autumn			Winter		
	Mean	SD	CV	Mean	SD	CV	Mean	SD	CV	Mean	SD	CV
2012–	10.57	1.43	0.13	18.66	4.76	0.25	14.45	3.22	0.22	6.45	1.48	0.22

2013

2013–
2014

2.25

1.56

0.69

6.41

4.13

0.64

5.46

0.31

0.05

2.03

0.44

0.21

Table 3. Eigenvector coefficients of hydrological and water physico-chemical parameters in relation to the 3 first axes of the PCA. PC1, PC2 and PC3 explained 47.1, 17.4 and 15.21% of data variability, respectively. Highest coefficient values for each factor are highlighted in **bold**; DIN: dissolved inorganic nitrogen, CV: coefficient of variation

Parameter	PC1	PC2	PC3
Freshwater discharge	0.68	−0.24	−0.16
DIN	−0.23	0.03	0.84
PO ₄	0.14	−0.56	0.64
Level	0.92	−0.16	−0.16
Temperature	−0.30	0.81	0.18
Salinity	−0.88	−0.29	0.04
Turbidity	0.74	0.47	0.33
Irradiance	−0.83	0.27	−0.20
Salinity CV ^a	0.83	0.33	0.06

^aProxy for water retention in the study area